

## PAPERS READ.

A CONTRIBUTION TO A FURTHER KNOWLEDGE OF  
THE CYSTIC CESTODES.

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(Plates III.-V.)

The following paper may for convenience be divided into three parts.

Part i. includes the descriptions of two new species of the genus *Piestocystis*, Diesing,—the first from the copper-head snake, *Hoplocephalus superbus*; the second, a somewhat remarkable proliferating form from the lizard *Lialis*—and the general considerations following therefrom.

Part ii. is a description of a new species of *Monocercus* from the earthworm *Didymogaster sylvatica*, Fl.

Part iii. contains an account of the development of the scolex of *Synbothrium*, a genus of *Tetrarhynchida*.

I must here express my great indebtedness to Prof. Haswell for his ever ready advice, and for much valuable assistance during the course of my work; and also my best thanks are due to Mr. Masters, Curator of the Macleay Museum, and to Mr. H. Throsby for the material in which the cysts described in Part i. were found; also I have to thank Herr W. Musmann for much assistance with the literature.

## PART I.

1. ON A NEW SPECIES OF *PIESTOCYSTIS* FROM *HOPLOCEPHALUS*  
*SUPERBUS*.

The cysts on which the following account is based were found imbedded in the peritoneum surrounding the intestine of a single specimen of the "copper-head" snake, *Hoplocephalus superbus*,

common in certain parts of New South Wales. The cysts when fresh appeared as opaque oval bodies, the largest of which measured 5 mm. in length and 4 mm. in breadth. Each cyst encloses a single *Cysticercus*, which fills up almost completely the cavity of the cyst, in this respect contrasting strongly with the *Lialis* cyst, in which, as will be seen in the following, the cyst cavity is very large and the one or more *Cysticerci* lie perfectly free within it.

*Structure of the cyst wall.*—In section (Fig. 1) the cyst wall is found to be of considerable thickness and to differ in structure in its inner and outer regions. The inner part, which immediately encloses the *Cysticercus*, is composed of a homogeneous layer (Fig. 1, *h. l.*) very similar in appearance and mode of staining to the cuticle of the *Cysticercus*. External to this homogeneous layer and occupying the central part of the cyst wall is a region (*l. l.*) having an irregularly laminated appearance and containing large spaces, probably lymph spaces. External to this and forming the outer layer of the wall is a feebly staining region of a fibrous nature (*f. l.*) and with numerous spaces. In the fresh cyst the outermost layers of the wall can be easily removed with needles, leaving the inner layer as a clear membrane closely surrounding the *Cysticercus*.

Seeing that the cyst wall is marked out by its optical characters and its histological structure into these two regions, I am inclined to attribute to each a distinct origin. The outer region, consisting of the laminated zone and the fibrous zone, is, I believe, derived from the peritoneum of the host by pathological change, while the inner homogeneous layer probably represents a direct derivative of the six-hooked embryo, and corresponds to the lining of the cyst in *Lialis*, to the so-called cyst of *Monocerci*—in a word, to what Villot\* terms the blastogen or blastogenic vesicle.

*Structure of the Cysticercus.*—When the *Cysticerci* are liberated from the cyst, they are found to be somewhat pear-shaped bodies

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\* "Mémoire sur les cystiques des Ténias." Ann. des Sci. Nat. Zool. 6me série, Tome xv. (1883).

broad at the anterior end, in which the head lies inverted, and tapering to a blunt rounded posterior end. They varied somewhat in size, the largest measuring 3 mm. in length and 2 mm. in thickness at the broader anterior end, while the smallest were 1.5 mm. in length and 1 mm. in thickness, exactly half the size of the largest. When examined under compression the *Cysticercus* is seen to possess numerous close-set calcareous corpuscles, uniformly distributed over the body. They are mostly in the form of short rods with rounded ends, measuring in greatest length .04 mm.; others have a more oval or rounded outline. At the broad end the head lies invaginated. It is provided with four large suckers whose cavities communicate with the cavity of invagination of the head. Hooks are altogether absent, but at the bottom of the invagination cavity of the head, situated centrally in what will in the everted condition form the apex of the head, is a small rounded body, representing a rudimentary frontal sucker (Fig. 2, *f. s.*). As the head was not readily everted in water, I have not been able to examine a completely everted *Cysticercus*. This is the more to be regretted, for in the everted condition the relations of the frontal sucker could have been more easily made out. It appears from the examination of preserved specimens that the suckers can be protruded separately. Fig. 2 represents a nearly median longitudinal section through such a *Cysticercus* with partially evaginated head, the knob-like mass projecting at the anterior end being one of the protruded suckers in section. In this section the invagination cavity appears as a wide opening, but transverse sections of a *Cysticercus* with the head fully inverted show that it is comparatively narrow and lined by cuticle continuous with the external cuticle of the body. It is filled up with a granular deeply staining material which is apparently derived from the coagulated fluid which surrounds the *Cysticercus*. Fig. 3 represents a section through the inverted head of a *Cysticercus* at the level of the suckers. Their walls are composed of numerous small radially elongated cells and their cavities open into the invagination cavity. The ground tissue immediately surrounding the suckers is seen to be disposed in a

circular manner, giving rise to a definite sheath (Fig. 3, *r. c.*) which surrounds the inverted head. This sheath represents the "receptaculum capitis" of Leuckart, concerning which he says,\* "The receptacle has least independence in the bladder worms with parenchymatous bodies such as we have seen in *Cysticercus* (*Piestocystis*) *variabilis* and its allies, for there it is not only connected with the mass of the head, but, like the ordinary body muscles, bound up with the tissue of the bladder." Along with the receptacle, mention must be made of the numerous muscular or elastic fibres which run through the body tissue. They are composed of a homogeneous substance which stains uniformly and shows no trace of cellular structure. In Fig. 3 in the receptacle they are seen to be more or less radially arranged, while in Fig. 2 some of the fibres are seen to take a longitudinal course, passing forwards like the similar fibres in the *Lialis Cysticercus*, to be inserted into the head.

The bladder cavity in this form is represented by an irregular cavity occupying the centre of what represents the caudal bladder of ordinary *Cysticerci*, and not distinctly marked off from the surrounding ground tissue. The cavity is filled by a granular material consisting of a homogeneous matrix with granules which stain deeply with cochineal, and which represent the products of degeneration of the original central tissue, which in the *Cysticercus* from *Lialis* (*seq.*) persists unaltered.

*Frontal sucker.*—The frontal sucker is situated medianly in the inner part of the invaginated head, in what will in the evaginated condition be its apex. In sections (Figs. 2 and 4), both by its structure and staining properties, it can readily be distinguished from the surrounding tissue. At its narrower anterior end is a slit-like aperture which places the cavity of the sucker in communication with the cavity of invagination of the head. The sucker cavity (Fig. 4, *s. c.*) is much wider than its opening, but is very shallow, so shallow, indeed, that the aperture and the cavity only

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\* "Parasites of Man," English Edition, p. 347.

extend through three thin sections, of which the middle one is represented in Fig. 4. The cavity is lined by a delicate layer of cuticle just as Monticelli describes\* for the terminal sucker of *Scolex polymorphus*. The wall of the sucker he describes as consisting of radial fibres similar to those of the suckers of Trematodes. In the form under consideration, nuclei are readily visible in the wall, but the cell boundaries could not be made out, nor were the radial fibres distinguishable.

In the tissue surrounding the sucker are numerous radially and circularly running fibres. The radial fibres correspond to what Monticelli calls† the retractors of the terminal sucker. Like the latter the radial fibres pass out from the central sucker and some of them can be traced to the inner sides of the lateral suckers. According to Monticelli, the retractors of the terminal sucker in *Scolex polymorphus* are inserted into the dorsal side of the four suckers. That the structure here termed the frontal sucker represents the similarly named structure in *Scolex polymorphus*, though in a somewhat reduced condition, is evident from the foregoing.

The morphological value of the frontal sucker of *Scolex polymorphus* is considered at some length by Monticelli in the paper already referred to.‡ He regards the frontal sucker and its retractors as homologous with the frontal sucker and its musculature in *Amphilina*, and as homologous with the buccal sucker of Trematodes, as representing in fact the lost digestive tract of Cestodes.

I quote his conclusions in full :—“In breve, saremmo per tutti i fatti esposti indotti ad ammettere una forma ancestrale primitiva trematodiforme di Cestode fornita di bocca ed intestino, il quale, è a poco a poco scomparso per effetto del parassitismo. E ad attestare

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\* “Contribuzioni allo studio della fauna elmintologica del Golfo di Napoli,” Mitt. Zool. Stat. Neap. B. viii. 1888, p. 114.

† *Loc. cit.* p. 118.

‡ *Loc. cit.* pp. 118 and 121.

la presenza di questo intestino scomparso, vi è in alcuni Cestodi adulti, molto semplici, una ventosa boccale con le sue glandole salivari e la sua muscolatura, come condizione permanente (*Amphilina*) ed in altri Cestodi: (1) allo stato larvale, in Cestodi meno differenziati, evvi una ventosa anteriore per struttura e funzione paragonabile alla ventosa dei Trematodi, con una muscolatura propria (scolici di Tetrabothridæ: Call., Tetrab., Phyll.) ed in quelli più differenziati (Tetrarhynchidæ) un rudimento di ventosa sotto forma di fossetta (*Anthocephalus elongatus*) nel quale sboccano le glandole salivari, e rudimenti muscolari alla estremità dello scolice (*Anth. elongatus* et *Ant. reptans*); (2) allo stato adulto poi vi sono ora dei rudimenti di ventosa anteriore (*C. corollatum*, *C. filicollæ*, *Rhynchob. corollatum*), ora delle glandole salivari (*Tetrabothrium longicollæ*), Zschokke, ora dei rudimenti muscolari (*Calliobothrium* e *Tenie*).”\* In view of these observations of Monticelli, it is interesting to find Grassi and Rovelli,† from a totally different standpoint, viz., that of the development of the Cysticercus of *Tænia elliptica*, instituting a comparison between the rostellum of certain Cestodes and the pharynx of Trematodes.

That the rostellum and frontal sucker are homologous structures is strikingly borne out by Leuckart's description‡ of the rudimentary rostellum of *Tænia saginata*. He says:—“So far then the rostellum of *Tænia saginata*, in spite of its comparatively weak development, possesses essentially the structure seen in the hook-bearing cystic tapeworms. But, while in the latter the rostellum is covered by a prominent layer of parenchyma in which the anterior processes of the hooks are embedded, this coating is represented in *T. saginata* only by an annular diaphragm, which lies as a lip on the outer wall of the above-mentioned lenticular mass. This is more or less markedly arched according to the curvature of the

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\* *Loc. cit.* pp. 122-123.

† Embryologische Forschungen an Cestoden, Centralb. f. Bact. u. Parasit. B. v. 1889, p. 376.

‡ *Loc. cit.* p. 434.

latter, and has in its centre an opening which is expanded below and appears sometimes rather deep, since the lenticular body has not unfrequently a depression in its anterior surface. This is the opening long since observed by Bremser and occasionally by other observers, and the appearance of which has given rise to the formerly prevalent idea that the tapeworms possessed a mouth opening between the suckers," and further he regards "this pore (frontal sucker), along with the muscular apparatus lying below it (the rostellum or bulbus), as the morphological equivalent of that sucker which is found between the lateral suckers, not only in Rudolphi's *Scolex* and the associated *Phyllobothria*, but also in some *Tæniadæ*."

Admitting then that the structure under consideration in *T. saginata* is the homologue of the frontal sucker, found in a more highly developed condition in other forms, and accepting Leuckart's further observation, viz., that the rostellum in the hook-bearing cystic worms passes through a developmental stage similar to that which is retained as the permanent condition in *Tænia saginata*, we have clear proof of the homology of the two structures. The disappearance of the hook-fundaments which surround the pore of the sucker in *T. saginata* is certainly due to degeneration, but in the sucker itself we have clearly the persistence in the adult of a developmental stage, early lost in the other hook-bearing *Tæniadæ*. These facts tend clearly to show that phylogenetically the frontal sucker is the older of the two structures, and that as specialisation has proceeded it has been replaced by the rostellum.

If this be so, then we must regard the condition in *Polycercus Didymogastri*s, where, as we have shown,\* the head, with the rostellum, arises in the centre of a cellular mass, as an example of the most highly specialised condition in the series.

*Excretory System*.—In the living *Cysticercus* examined under compression, the longitudinal trunks of the excretory system were

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\* "On *Polycercus*," P.L.S.N.S.W. (2), Vol. viii. p. 373.

readily visible. Two large vessels are present on either side and extend throughout the whole length of the body. Numerous smaller canals were also visible, which seemed to communicate with one of the main trunks on either side. The canals contained a liquid in which were suspended bright refractive granules, rounded or oval in form, in rapid circulation. The direction of the currents in the compressed *Cysticercus* was of an inconstant character; at one moment the liquid with the granules might be seen flowing towards the head, then the direction of the current would be reversed and the granules flow towards the posterior end.

These observations, taken from my rough notes made at the time of examination, do not agree with Monticelli's account\* in *Scolex polymorphus*. Whether this reversal of the direction of the current is a normal feature in our *Cysticercus* or abnormal and due to the great compression to which it must be subjected before any of the internal details can be made out, I am unable to say. But Monticelli's observation that by an undulatory movement of the walls of the descending trunks the contained liquid transports the calcareous corpuscles to the head, inclines me to the latter belief.

The refractive granules, referred to above, represent calcareous corpuscles similar to those Monticelli has described as existing in the descending trunks of *Scolex polymorphus*, and which he regards as similar to those described by Fraipont in the accessory branches of the great trunks of the excretory system of *Diplostomum*.

Fraipont† in *Scolex trygonis pastinacæ* describes two longitudinal vessels on either side, of which one is smaller than its neighbour. The two larger vessels open posteriorly into the pulsatile vesicle, while anteriorly they curve back to form the smaller vessels which at the posterior end resolve themselves into

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\* *Loc. cit.* p. 126.

† "Recherches sur l'appareil excréteur des Trématodes et des Cestodes," *Archives de Biologie*, T. ii. 1881, p. 5.

a network around the pulsatile vesicle. The larger vessels he terms the descending trunks, and the smaller the ascending. Monticelli confirms\* Fraipont's description as to the difference in size of the vessels and also as to the mode of termination of the vessels.† Pintner,‡ on the other hand, maintains that all the four canals in the young forms terminate in the contractile caudal vesicle, and such is the condition in the *Cysticercus* under consideration. In sections, the larger descending (Fig. 3, *d. v.*) and the smaller ascending canals (*a. v.*) can be readily distinguished, two on each side. They differ not only in size but in the thickness of their walls. Both are lined by a cuticular membrane, which, however, is thicker and much more distinct in the case of the smaller ascending canal. Posteriorly the two vessels on each side unite with each other, then pass inwards and backwards to open into a short terminal canal which communicates with the exterior. The terminal canal is lined by a very definite cuticle, which when traced back is found to grow thicker and to become continuous with the external cuticle of the *Cysticercus*.

*Structure of the cuticle and the subcuticular layer.*—The cuticle (Figs. 5 and 6) consists of a thick layer of uniform depth, which with cochineal shows a differentiation into an outer thicker layer and an inner thinner more deeply staining layer. The external surface is smooth, no hair-like appendages being present, as Monticelli§ describes for *Scolex polymorphus*.

As Leuckart describes|| for Cestodes generally, there is, immediately below the cuticle and in close contact with it, a thin layer of circularly disposed elastic fibres (Figs. 5 and 6, *c. f.*); internal to this circular layer is, in transverse sections, a layer of bright refractive bodies (Fig. 5, *l. f.*), separated from each other by interspaces. They represent the transverse sections of a layer of

\* *Loc. cit.* p. 124.

† *Loc. cit.* p. 127.

‡ As quoted by Monticelli.

§ *Loc. cit.* p. 133.

|| "Parasites of Man," p. 290.

longitudinally running elastic fibres. The outer circular layer and the inner longitudinal together constitute the "musculo-dermal" layer of Leuckart, but which is perhaps here better termed a "dermo-elastic layer." Griesbach describes\* in *Solenophorus megalcephalus*, below the cuticle, a similar layer of circular elastic fibres, while the longitudinal fibres correspond to his subcuticular "Langsmuskeln."

Internal to the "dermo-elastic" layer is the layer termed by various authors subcuticula, subcuticular or hypoderm layer, or the layer of matrix cells.

The subcuticula of the *Hoplocephalus Cysticercus* is composed of a layer of radially elongated cells, which appear somewhat triangular in transverse section (Fig. 5, s. c.), with their broad ends directed outwards and their narrow ends inwards; in longitudinal section (Fig. 6, s. c.) they appear more spindle-shaped and their narrow ends are prolonged for some distance into the body tissue. They possess deeply staining nuclei, which, as Steudener has noted generally for Cestodes, may be situated in any part of the cell, sometimes near the middle, at other times nearer the base or apex, "so that they appear not in a line but alternating in a somewhat broad zone."†

As Roboz‡ finds in *Solenophorus megalcephalus*, the cells composing the subcuticula do not abut directly on one another or on the "dermo-elastic" layer, but are separated from each other and from the dermo-elastic layer by a finely granular matrix (Fig. 5, m.). Monticelli§ apparently not recognising the existence of this intercellular matrix, inclines to the belief that the spaces between the cells are due to the effect of the reagents used, and very probably also, as Pintner says, to the state of contraction or extension

\* "Beiträge zur Kenntniss der Anatomie der Cestoden," Archiv f. Mik. Anat., Band xxii. 1883, p. 571.

† Leuckart, "Parasites of Man," p. 288.

‡ Zeit. f. wiss. Zool. xxxvii.; Abstract Journ. Roy. Mic. Soc. Vol. ii. Ser. 2nd, 1882, p. 785.

§ *Loc. cit.* p. 136.

of the body. No doubt the latter factor does, to some extent, influence the closeness or remoteness of the subcuticular cells, but that it does so in only a very slight degree is shown by the fact that in invaginated Cysticerci (*i.e.*, in the most contracted condition) these spaces are always recognisable between the cells.

*Ground tissue.*—The ground tissue (the ground parenchyma, ground substance, body parenchyma, of various authors) consists, as Griesbach describes\* for *Solenophorus* and Hamann† for *Tania lineata*, of a granular matrix, in the outermost part of which the subcuticular cells lie embedded. It contains, internal to the subcuticula, numerous rounded, fusiform or stellate cells, the nuclei and cell bodies of which are clearly distinguishable.

Certain of these cells lying nearer the subcuticula have an oval nucleated cell body, which is produced on opposite sides into two narrow processes, the outer of which can be traced into the space between two adjacent subcuticular cells and is probably inserted into the “dermo-elastic” layer; the inner process passes for some distance into the ground tissue. These cells probably function as muscular cells. Zograf,‡ in *Solenophorus megacephalus* and *Trienophorus nodulosus*, describes and figures cells “de forme étoilée, avec leurs longues excroissances en forme de rayons qui, d’un côté, s’élèvent entre les cellules de la matrice jusqu’ à la cuticle, et, de l’autre, s’enfoncent dans le parenchyme du ver et s’y rattachent aux cellules semblables du tissu conjonctif du parenchyme.” These star-shaped cells closely agree in their relationships with the cells described above. With the exception of the elastic fibres already described as occurring in the ground tissue, no distinct bundles of longitudinal muscle fibres were recognisable.

\* *Loc. cit.* p. 527.

† *Zeit. f. wiss. Zool.* xlii. 1885; *vide* Rolleston’s “Forms of Animal Life,” 2nd ed. p. 226.

‡ “Les Cestodes, offrent-ils des Tissus ectodermiques ?” *Archives Zool. Exp. et Gen.* 2nd Ser. T. x. 1892, No. 3, p. 339.

The inner region of the matrix contains scattered nuclei, the cell bodies of which were not distinct. Ill-defined spaces occur here and there in the matrix, but the definite lacunæ figured by Griesbach\* for *Solenophorus* do not exist in this form.

Calcareous corpuscles occur throughout the whole thickness of the body tissue, but are specially aggregated in a zone situated some distance below the subcuticula.

In Cysticerci which have been stained by an acid fluid, such as Ehrlich's acid hæmatoxylin, and afterwards treated with acid alcohol, these bodies are dissolved and for the most part disappear. Their position is, however, indicated by circular spaces (Fig. 5, *r. c. c.*) surrounded by a wall and clearly marked off from the surrounding matrix.

Prof. Haswell,† in reference to the calcareous corpuscles in the parasitic flat-worm from the frog, says:—"From their appearance when acted on by dilute acid, it would appear that the two parts of the corpuscle are of different composition, the inner part becoming, before it is entirely dissolved, converted into a cluster of granules, while the outer part never becomes granular, but only gradually becomes less and less distinct till a fine outline alone remains." In sections treated with acid reagents, the cluster of granules representing the inner part of the corpuscle can in many cases be distinguished lying in a cavity which is bounded by a wall representing the wall of the cell in which the corpuscle is formed. At one point on the wall the original cell nucleus can be recognised.

Immediately external to the zone containing the calcareous corpuscles, in sections from Cysticerci which have been stained with a neutral fluid such as cochineal, numerous round spaces can be seen, containing a number of rounded or oval granules (Fig. 6, *c. n. c.*), similar in optical characters and staining properties to

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\* *Loc. cit.* Taf. XXI. figs. 1 and 2.

† P.L.S.N.S.W. Vol. v. (2), p. 664.

the ordinary calcareous corpuscles. In some cases the spaces contain one or more large granules with a number of small ones, in others the small granules are alone present. Their very definite form goes against the belief that they are due to the action of the fixing fluid (corrosive sublimate) or the staining fluid (cochineal). It may be that they represent cells which produce instead of one large corpuscle, a number which lie free in their cavities.

## 2. ON A PROLIFERATING SPECIES OF *PIESTOCYSTIS* FROM *LIALIS*.

A living specimen of the widely distributed but somewhat rare lizard *Lialis Burtonii*, Gray, for which I am indebted to Mr. Masters of the Macleay Museum, was found on dissection to be infected with cysts of a somewhat remarkable character. Each cyst contained from one to three *Cysticeri*, which lay quite free in the cavity of the cyst. In the fresh condition the cysts appeared as vesicular elevations of the wall of the small intestine, along the whole length of which they were found, usually placed singly, but in some cases two occurred in close apposition, with a common wall between them. The largest cyst observed measured 1.75 mm. in diameter. Through the kindness of Mr. R. Etheridge, Junr., Acting Curator of the Australian Museum, and of Mr. Masters, I had the opportunity of examining six spirit specimens of *Lialis*, and in two of these the cysts were again encountered, occupying the same position as described for the living form. When the living cysts are removed from the wall of the intestine and the cyst wall ruptured with needles, the cyst collapses owing to the escape of the *Cysticeri* and the fluid which surrounds them. In the fresh specimen examined, two *Cysticeroids* were found in the greater number of the cysts, one usually larger than the other; in a few one *Cysticerus* only was found, but seeing that in cysts containing two *Cysticeri* one was larger than the other, and also judging from certain appearances seen in entire cysts mounted in glycerine and in a series of sections, I am inclined to believe that the cysts with only one *Cysticerus* had

not advanced so far in development as the cysts containing two. In one of the spirit specimens examined, a cyst was found containing three equally and fully developed *Cysticerci* (Fig. 7).

*Structure of the cyst wall.*—The outer wall of the cyst is composed of a fibrous layer (Fig. 8, *f. l.*) continuous with the muscular layer of the wall of the intestine and doubtless formed from it by the replacement of its muscular elements by fibrous tissue. It contains scattered cells, blood vessels, and lymph spaces and is covered externally by peritoneum. Internal to this fibrous outer wall and lining the cavity of the cyst is a thin layer of slightly staining homogeneous substance, with flattened nuclei on its inner face (*h. l.*). As in the case of the cyst wall of the *Cysticercus* from *Hoplocephalus*, I attribute to these two well-defined parts of the wall a distinct origin. The outer wall is a product of the tissues of the host, while the thin inner lining of the cyst cavity, together with the cellular network in its interior (*seq.*), are the direct derivatives of the six-hooked embryo, representing the prosclex or blastogen of Villot.

The cavity of the cyst is occupied by a branching network of cells, the nucleated cells from which the anastomosing processes arise being situated irregularly in the angles between the meshes. Round the periphery of the cavity of the cyst the processes of these branching cells become continuous with the inner lining of the cyst wall, a fact which supports the view expressed above, that the inner lining of the cyst is an integral part of the parasite and not derived from the host.

*Structure of the Cysticerci.*—The *Cysticerci* lie embedded in this network, and, as they occur naturally in the cyst, are small rounded or oval bodies, about .75 mm. in diameter, and with the head invaginated at the broader anterior end (Fig. 9). When the cyst wall is ruptured and the *Cysticerci* allowed to escape in a drop of water, the head is immediately evaginated and they begin to creep about actively; the change of shape is so remarkable that the movement might almost be described as amœboid.

The evaginate *Cysticerci* (Fig. 10) measure from 1.25 to 2 mm. in length. In each can be distinguished an anterior or head end, conical in form and provided with four large well-marked protrusible suckers, which passes gradually, by way of a narrow neck region, into the posterior much wider and longer region, which Leuckart considers as the homologue of the caudal bladder of the ordinary bladder worms.

The whole body is invested in a layer of cuticle which in the head region is covered by numerous very minute backwardly directed spinules .002 mm. in length. Hooks are altogether absent. Numerous minute black points are visible all over the cuticle. These may be the external openings of pore canals, but sections did not reveal their existence in the cuticle. The posterior part of the *Cysticercoid* contains very numerous uniformly distributed calcareous corpuscles, which are most abundant in the superficial layers of the body tissue, but occur in the more central tissue as well. They vary in shape from round to angular and are almost entirely confined to the posterior region, only a few being found between the suckers of the head.

The excretory system opens at the posterior end of the *Cysticercus* by a short tube, which in the living form is seen to be pulsatile. It is lined by a continuation of the outer cuticle and in sections is visible as a minute tube with a cuticular wall passing forwards for a short distance.

In the inverted *Cysticercus* the head lies inverted in the central tissue of the body, and, as in the typical bladder worm, the cavity of invagination is in free communication with the exterior, and into it the cavities of the four suckers open. Fig. 11 represents a transverse section at the level of the suckers. Just as in the case of the *Hoplocephalus Cysticercus*, the invaginated head is surrounded by a thick envelope of circularly arranged tissue representing the receptacle of the head. In the superficial region of the body tissue in the posterior part of the *Cysticercus*, and especially clear in *Cysticerci* preserved in Flemming's Fluid, are bundles of elastic fibres which run towards the head, and as they

do so widen out to become inserted into it. They, like the similar longitudinal fibres in the *Cysticercus* from *Hoplocephalus*, probably have to do with the invagination of the head.

In histological structure the *Cysticercus* under consideration agrees closely with the *Cysticercus* from *Hoplocephalus*, in which I have gone into detail more fully. Below the cuticle the outer circular and inner longitudinal layers of elastic fibres can be recognised, and internal to these the subcuticula, consisting of a richly nucleated layer of radially elongated cells, whose outlines, however, owing to the small size of the *Cysticercus*, are difficult to make out.

The ground tissue is composed of a matrix with scattered nuclei, but here, as distinguished from the *Hoplocephalus Cysticercus*, the posterior part is solid, there being no indication of a central cavity. In this respect it agrees with two forms mentioned by Leuckart,\* "one from the sub-epidermal tissue of the nightingale and another from the body cavity of *Lacerta vivipara* (*Piestocystis Dithyridium*, Diesing)," in which no bladder cavity is present.

As to the development of the *Cysticerci*, the material at my disposal did not offer any certain developmental stages, but it seems probable that the *Cysticerci* arise by a process of proliferation from the thin inner lining of the cyst cavity, which, together with the cellular network in the interior of the cyst, I interpret as the direct derivative of the six-hooked embryo, representing the blastogen of Villot. The small mass of cells attached to the lining of the cyst in Fig. 8 probably represents the first stage in development of one of the *Cysticerci*. This bud probably increases in size, becomes separated from the wall, and comes to lie free in the cavity of the cyst, forming a mass of cells such as are seen in the right hand corner of the cyst cavity in Fig. 8. Later, round this mass the cuticle is differentiated, and finally by an invagination at one end the head is developed, the suckers developing on the interior of the invagination cavity.

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\* "Parasites of Man," p. 343.

## GENERAL CONSIDERATIONS.

Diesing\* divides the cystic forms into four genera :—(1) *Echinococcus*, (2) *Cœnurus*, (3) *Cysticercus*, (4) *Piestocystis*. With the two latter we are for the present alone concerned.

According to Diesing the presence or absence of hooks serves to distinguish the genus *Cysticercus* from the genus *Piestocystis*; the Cysticerci are armed forms, the Piestocystes unarmed, and it is clearly among the unarmed Piestocystes that we must look for the relationships of the two forms described in the foregoing; they are both the cystic forms of hookless *Tæniæ*.

Villot,† basing his classification on the mode of formation of the caudal bladder, has divided the cystic forms into two groups. His first group includes cystic forms whose caudal vesicle arises from the prosclex by simple growth and modification of structure, without, strictly speaking, the production of any new part. His second group includes cystic forms in which the caudal vesicle arises from the prosclex by a process of budding, *i.e.*, by the addition of a new part. In the first group he includes the three genera, *Cysticercus*, *Echinococcus*, and *Cœnurus*, and it is with the first of these genera, with the Cysticerci properly so-called, that he classes the forms included in Diesing's genus *Piestocystis*. He says‡ :—“L'état inerme, pas plus que l'état armé, ne peut caractériser une coupe générique parmi les Cystiques; et il est bien évident que le groupe des *Piestocystis* doit disparaître de la nomenclature.” In support of this view he instances the case of *Tenia saginata*, a form which in the adult has no hooks and only a rudimentary (persistently embryonic) rostellum, but whose affinities structurally are with the armed *Tæniæ*.

Leuckart,§ however, has shown that the Cysticerci of this form, “although the descendants and young forms of a hookless tape-

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\* *Systema Helminthum*, Vol. i. p. 478.

† *Loc. cit.* “Cystiques des Ténias.”

‡ *Loc. cit.* p. 5.

§ *Loc. cit.* p. 463.



worm, are furnished with a distinct though small rostellum and with the rudiments of hooks"; and further Nitsche, according to Leuckart,\* has occasionally observed, in the adult form, these rudimentary hooks. In view of these facts, Villot's opinion, in so far as it rests on the case of *T. saginata*, loses its value.

It may now be well to institute some comparison between the Cysticeri properly so-called and the two forms described in the foregoing as representing the genus *Piestocystis*.

The unarmed *Piestocystes* are not only sharply marked off from the Cysticeri properly so-called by the absence of hooks, but also by their general structure. The retractile more or less conical head, destitute of hooks and provided with four large and well-marked suckers, is characteristic, as also is the elongated posterior portion usually interpreted as representing the caudal vesicle.

According to Villot, four parts can be distinguished in an ordinary Cysticercus: (1) the cyst, (2) the head, (3) the body, (4) the caudal vesicle. The cyst is in the Cysticeri properly so-called an adventitious structure derived from the host, and having no genetic connection with the enclosed Cysticercus, and so may be left out of consideration in the present connection. The Cysticercus itself consists of the three parts—head, body, and caudal vesicle. If we, with Leuckart and other observers, consider the posterior part, in which the head is invaginated, in these unarmed forms, as representing the caudal vesicle, what corresponds to the body of the ordinary Cysticercus? It seems to be represented by the muscular sheath which immediately surrounds the invaginated head and which has in the foregoing been regarded as comparable to the "receptaculum capitis" of Leuckart. The "receptaculum capitis" of Leuckart is, as Villot has shown,† formed by the internal of the two layers into which the somato-cephalic bud of the developing Cysticercus separates. From the internal layer (the receptaculum capitis) the inner wall of the body is derived, while from the external are derived the outer wall of the body

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\* *Loc. cit.* p. 435.

† *Loc. cit.* p. 14.

and the head of the *Cysticercus*. In the forms under consideration, these two layers enclosing an interparietal cavity do not appear to be represented, and further, as Leuckart states,\* the sheath or so-called receptacle is in these forms "not only connected with the mass of the head, but, like the ordinary body muscles, bound up with the tissue of the bladder." Hence, if this sheath be taken as representing the body of the *Cysticerci* properly so called, we may take it as characteristic of the genus *Piestocystis* that the body, unlike that of the *Cysticerci* properly so-called, is not represented by a part distinct from the caudal vesicle.

The absence of a well-marked bladder cavity containing fluid is also a noteworthy feature and one which has given rise to the name parenchymatous bladder worms for these forms. The cavity may be entirely absent or it may be represented by an irregular space bounded by thick walls. With reference to this feature Leuckart says†:—"With the loss of the bladder cavity most of the characteristic peculiarities of the bladder worms have been also lost, so that it is hardly possible to distinguish these forms from developed bladder worms with evaginated heads. In fact, even in spite of the attached caudal bladder, such a form as that represented on Fig. 185c looks exactly like a young still unsegmented tapeworm."

The *Cysticercus* which most closely approaches these parenchymatous forms in the absence of a distinct bladder cavity is that of *Tenia elliptica (cucumerina)*, but it is at once distinguished from them by the possession of hooks, and further, as Grassi and Rovelli have shown,‡ the fully formed *Cysticercus* represents only the anterior part of the six-hooked embryo, the posterior part which forms the tail being lost on the *Cysticercus* reaching maturity.

As one of the characters of the genus *Piestocystis*, Diesing gives the absence of a rostellum, but its homologue, the frontal

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\* *Loc. cit.* p. 347.

† *Loc. cit.* p. 343.

‡ "Embryologische Forschungen an Cestoden," *Centralb. f. Bakt. u. Parasit.*, Band v. 1889.

sucker, is found in the form from *Hoplocephalus*, and Van Beneden\* in a form, *Milina grisea*, from the intestine of *Vespertilio murinus* and *serotinus*, and which evidently belongs to the genus *Piestocystis*, describes an unarmed bulb as existing between the four suckers, and also Bellingham,† in a *Cysticercus* from *Cobitis barbatula*, has observed a similar unarmed proboscis, so that this character of Diesing no longer holds. The presence of a posterior pulsatile excretory tube and of numerous calcareous corpuscles in the caudal vesicle are features of lesser importance.

Thus, in the absence of hooks, of a distinctly differentiated body, and of a proper bladder cavity, these forms are sharply marked off from the *Cysticerci* properly so-called.

Returning now to the consideration of the cyst, in *Cysticerci* properly so-called it is, as already remarked, a wholly adventitious structure, being derived from the tissues of the host and having no genetic connection with the enclosed *Cysticercus*. In the unarmed forms considered in the preceding, the inner lining of the cyst in that from *Hoplocephalus* and the inner lining of the cyst, together with the cellular network in the interior of the cyst from *Lialis*, are, in our opinion, the direct derivatives of the six-hooked embryo, and correspond to the so-called cyst of *Monocercus arionis* and of *M. glomeridis*, and to the cellular cyst of *Monocercus Didymogastri*s (cf. Part ii.), representing in fact the proscotex or "blastogen" of Villot.

This consideration, viz., that, in the unarmed forms under consideration, we have, surrounding the *Cysticerci* and forming part of the cyst wall, a part which is the direct derivative of the six-hooked embryo, and which is not found in any *Cysticercus* properly so-called, is alone sufficient justification for removing them from Villot's genus *Cysticercus*, and they certainly have no genetic connection either with *Echinococcus* or *Cœnurus*.

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\* "Les Parasites des Chauves-souris de Belgique," Mém. de l' Acad. Roy. de Belgique, T. xl. 1873, as quoted by Moniez, "Essai Monographique sur les Cystiques," p. 144.

† "On Irish Entozoa," Ann. Mag. N.H. Vol. xiv. p. 398.

Superficially there is a slight similarity between an isolated *Echinococcus* head and, say, the *Cysticercus* from *Lialis*, but detailed comparison shows they have little in common. Leuckart,\* after referring to the similarity in disposition between the enclosing portion of the *Echinococcus*-head and the caudal bladder of a *Cysticercus*, says:—"Nevertheless it is impossible to regard the capsular envelope of the retracted *Echinococcus*-head as a caudal bladder, and that not only because it forms an integral part of the head, and is included in the body of the future tapeworm, but more especially because of its entirely different origin." In the foregoing we have considered the part in which the head is invaginated in these forms as representing the caudal vesicle and body, and that it does not become part of the future tapeworm, Von Linstow's† observation of the commencement of segmentation in the part immediately succeeding the head in *Cysticercus* (*Piestocystis*) *Dithyridium* strikingly bears out.

Multiplication in the genus *Piestocystis* takes place, according to Diesing, by a process of external proliferation from the caudal vesicle. This method of multiplication certainly does not hold good for the forms under consideration, and Villot‡ agrees with Leuckart§ in believing that the so-called buds are malformations due to purely mechanical causes; still it is possible that certain species do multiply by external proliferation. In the two forms under consideration internal proliferation undoubtedly takes place, in the first one *Cysticercus* only is formed, in the second three may be thus formed. Here the caudal vesicle does not proceed from the prosclex by simple growth and modification of structure as in Villot's genus *Cysticercus*, but it represents a secondarily formed structure derived by internal proliferation from the prosclex, which remains persistent in the form from *Hoplocephalus* as the inner lining of the cyst cavity, and in the form from *Lialis*

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\* *Loc. cit.* p. 604.

+ "Neue Beobachtungen an Helminthen," *Archiv f. Naturgesch.*, B. i. 1878, p. 222.

‡ *Loc. cit.* p. 22.

§ *Loc. cit.* p. 356.

as the inner lining of the cyst cavity together with the cellular network in the interior of the cyst.

The two forms under consideration are thus brought into close relationship with certain forms included in Villot's second group, but they agree so closely with one another and differ so widely in other respects from the Cysticercoïds that it seems advisable to associate them together in Diesing's old genus *Piestocystis*.

Leuckart\* regards these parenchymatous forms as in many ways connecting the Cysticercoïds with the ordinary bladder worms, and this is the view we here adopt. In their general structure they are certainly more nearly related to the Cysticercoïds properly so-called than to the Cysticercoïds, while at the same time the presence of the surrounding blastogen is a character they share in common with certain of the latter.

Finally, then, we hold the genus *Piestocystis* to include unarmed forms, intermediate between the Cysticercoïds properly so-called and the Cysticercoïds; and which are produced, one or more in number, by proliferation of the blastogen (proscölex).

The Lialis Cysticercoïd may be termed *Piestocystis Lialis*, and the Hoplocephalus Cysticercoïd *Piestocystis Hoplocephali*.

## PART II.

### ON A *MONOCERCUS* FROM *DIDYMOGASTER*.

While examining specimens of the earthworm *Didymogaster sylvatica*, Fl., for the *Polycercus* described by Prof. Haswell and myself in a previous part of these Proceedings,† one individual was found to be infected by a Cysticercoïd belonging to the allied genus *Monocercus*, for which I propose the name of *Monocercus Didymogastri*. The generic name *Monocercus* was proposed by Villot‡ for cystic forms of the type of *Cysticercoïd arionis*, in

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\* *Loc. cit.* p. 655.

† P.L.S.N.S.W. Vol. viii. p. 365.

‡ "Mémoire sur les Cystiques des Ténias," Ann. des Sci. Nat. (6), T. xv. 1883, p. 35.

which the blastogen (prosclex) gives rise by endogenous budding to a single caudal bladder, as distinguished from the genus *Polycercus*, in which, according to Villot, a number of caudal bladders are similarly produced.

*Structure of Monocercus Didymogastris.*—The *Monocerci* lie embedded in the wall of the intestine, generally in the superficial layers. They appear to the naked eye as small rounded elevations of a whitish colour, which vary considerably in size, the largest observed measuring .5 mm. in diameter and the smallest .18 mm. Each (Fig. 12) consists of two very distinct parts: (1) An outer clear cellular portion which we may provisionally term the cyst, and which surrounds (2) a central more opaque portion, the Cysticeroid proper. Considering these two parts separately, and first as to the outer portion. In section it is found externally to consist of a homogeneous membrane apparently of a cuticular nature and which stains more deeply than the cuticle of the Cysticeroid. Internal to this cuticular membrane is a single layer of large cells, each containing protoplasm with refractive granules and a nucleus; their walls are continuous with the outer membrane and stain similarly to it. In the possession of this well-defined surrounding layer of cells, in the fully developed Cysticeroid, *Monocercus Didymogastris* appears to differ from all previously described forms belonging to this type. In *Cysticerus arionis*, Leuckart\* describes the Cysticeroid as surrounded by a true connective tissue cyst derived from the host. But Moniez† says:—"Le kyste dans lequel est enfermé le Cysticerque de l'*Arion* est pour nous, un produit du parasite lui-même et non une sécrétion de l'hôte." He, however, describes the cyst as consisting of concentric layers, an observation which Villot shows,‡ from the study of *C. arionis* and *C. glomeridis*, to be incorrect. According to him—"Le soi-disant kyste des Monocerques est, en réalité, une

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\* "The Parasites of Man," English Edition, p. 361.

† "Essai Monographique sur les Cysticerques," Travaux de l'Institut Zoologique de Lille, T. iii. fasc. 1, p. 74.

‡ *Loc. cit.* p. 38.

enveloppe très fragile, composée d'une mince cuticule et d'une couche sous-jacente de nature cellulaire." This subcuticular layer he describes as consisting of small groups of fine granules, separated from each other by a hyaline border and evidently representing a layer of cells in process of degeneration. Villot's observations receive ample confirmation from the form under consideration. There is here, just as in *C. arionis*, a layer of cuticle externally, and an underlying cellular layer, which, however, in the case of our *Monocercus*, shows no signs of degeneration. Accepting Moniez's view that the cyst belongs to the Cysticeroid itself, what does it represent? With Villot I agree in regarding it as the blastogen or blastogenic vesicle (prosclex), which by internal differentiation, either by budding or some process of separation, gives rise to the Cysticeroid proper. The Cysticeroid, then, together with the outer cellular layer, the blastogen, represent the entire product of the six-hooked embryo.

We pass now to the consideration of the second part of our *Monocercus*, the Cysticeroid proper.

Each is an ovoid body measuring from .15-.3 mm. in diameter. It lies perfectly free in the centre of the surrounding layer of cells. There is no connection nor any sign of connection between the outer wall and the Cysticeroid. Villot\* believes that in *Cysticercus arionis* he has seen, at the posterior part of the caudal vesicle of the Cysticeroid and the cyst, traces of an original connection in the form of "une sorte d'ombilic ou de dépression infundibuliforme." No such indication of an original connection is to be seen in the case of *Monocercus Didymogastri*; if it ever existed no trace of it remains in the fully-formed Cysticeroid. This fact suggests that the Cysticeroid, instead of arising from the prosclex by a process of budding, arises by the separation of the more central cells from a peripheral layer. The latter forms the outer layer of cells, while the central mass gives rise to the Cysticeroid by differentiation, probably in a manner similar to

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\* *Loc. cit.* p. 38.

what we have described\* in the development of an individual Cysticeroid in *Polycercus*. And I may here add that our observations on the development of the Cysticeroid in *Polycercus Didymogastri*s strikingly confirm Villot's view that the position of the head in Cysticeroids of the type of *Cysticercus arionis* is the primitive one and not secondary as Leuckart† believes.

When the Cysticeroid is examined in the fresh condition, it is seen to possess numerous uniformly diffused calcareous corpuscles .01-.012 mm. in diameter. At one end, the anterior, is a slight depression indicating the aperture of evagination of the head.

In sections the three parts found in all Cysticeroids of this type can be readily distinguished.‡ These parts are: (1) the head, (2) the body, (3) the caudal vesicle. The head forms a somewhat conical mass lying invaginated in the body, and with the blunt apex of the cone pointing to the aperture of evagination of the head. It bears on its sides four large and well-marked suckers, and in its centre lies the retracted rostellum, the anterior end of the latter forming the blunt apex of the head.

The head is covered by a definite cuticle and is composed of a dense mass of small-celled tissue. The suckers are composed of rounded cells, radial and circular fibres not being recognisable.

The rostellum is stout, thickest in its middle region, and with blunt anterior and posterior ends. It extends to near the posterior end of the head, terminating on a level with the posterior border of the suckers. It is composed of rounded cells larger and clearer than those of the rest of the head. Surrounding it is a thin sheath of a cellular nature, apparently corresponding to the muscular receptacle of other forms (*cf. Polycercus Didymogastri*s), but distinct muscular fibres were not recognisable in it. At the anterior end of the rostellum are the small hooks, sixteen to

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\* P.L.S.N.S.W. 2nd Series, Vol. viii. p. 365.

† *Loc. cit.* p. 362.

‡ Villot, "Metamorphoses des Ténias des Musaraignes," *Ann. des Sci. Nat.* (6), T. viii. 1878, p. 5.

twenty in number, and arranged in a single row. Each hook (Fig. 13) has a total length of  $\cdot 03$  mm. and is provided with an internal root ("dent," "Hypomochlion," or "talon") and an anterior root (Leuckart's "posterior process," Villot's "manche"). The anterior root, which is inserted into the tissue of the rostellum, runs forwards in a line with the free part of the hook (Villot's "lame"), while the internal root runs backwards almost parallel with the free part. The free part of the hook is  $\cdot 018$  mm. long, the internal root  $\cdot 0125$  mm., and the anterior root  $\cdot 012$  mm.

The great development of the internal roots of the hooks of *Monocercus Didymogastri*s may be taken as their most striking characteristic, and that they differ most markedly in form from those of *Monocercus arionis* and *M. glomeridis* a comparison of Fig. 13 with Villot's figures\* will clearly show.

The posterior part of the head, behind the posterior end of the rostellum and the suckers, may be taken to represent the neck. This neck region becomes continuous with a thin layer of deeply staining small-celled tissue, which passes forwards, completely enclosing the head. This represents the second part of the Cysticercoid—the body. Anteriorly it becomes continuous at the aperture of evagination with the outer wall of the Cysticercoid. The outer wall represents the third part of the Cysticercoid—the caudal bladder. In sections it is to be clearly distinguished from the layer forming the body. It is composed of a larger-celled tissue and does not stain so deeply with hæmatoxylin, and to it the calcareous bodies, distributed throughout its thickness, are almost entirely confined. Externally it is covered by cuticle, which, at the aperture of evagination, turns in, becoming continuous with what will, in the evaginated Cysticercoid, be the external cuticle of the body. Both in its histological structure and in its relations to the other parts of the Cysticercoid, this outer wall clearly corresponds to the caudal bladder of the ordinary Cysticerci.

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\* *Loc. cit.* pl. xii. figs. 10 and 11.

Grassi and Rovelli\* regard the outer wall as formed by the tail, the part on which in the *Cysticercus* of *Tenia elliptica* they find the hooks of the embryo are borne. "In ihnen (*C. arionis*) ist die äussere Wand, unserer Meinung nach, vorzugsweise von dem Schwanze gebildet, da sich die Haken auf der äusseren Wand oder auch auf dem Grenzpunkte zwischen der äusseren Wand und inneren Wand befinden (Meissener, Leuckart, Moniez)." They base their belief on the observations of Meissener, Leuckart,† and Moniez,‡ who assert that they have seen the hooks of the embryo lying on the caudal vesicle or on the body. With reference to these statements, however, Villot remarks §:—"Nous sommes persuadé qu' on a pris pour les crochets de l'hexacanthé quelque portion des fibres élastiques, très réfringentes, que l'on observe sous la cuticle de la vésicule caudale."

If we regard the so-called cyst (blastogenic vesicle) as the direct derivative of the six-hooked embryo, then, as Villot further says,|| "Les véritables crochets du Proscœlex doivent être cherchés sur le kyste." In view of these considerations, Grassi and Rovelli's interpretation falls to the ground.

Finally, it may be added that the hosts of Cysticercoids of this type have now been found among the Mollusca, the Myriapoda, and the Chætopoda.

### PART III.

#### ON THE DEVELOPMENT OF A TETRARHYNCH SCOLEX BELONGING TO THE GENUS *SYNBOTHRIUM*.

The cysts on which the following account is based were taken from the peritoneum surrounding the intestine of the jew-fish, *Sciaena aquila*. The form under consideration closely agrees with

\* "Embryologische Forschungen an Cestoden," Centralb. f. Bact. und Parasit., Band v. 1889, p. 404.

† *Loc. cit.* p. 361.

‡ *Loc. cit.* p. 74.

§ *Loc. cit.* p. 39.

a cyst from the liver of *Cybius regale*, described by Linton\* under the name of an embryo *Tetrarhynchobothrium*, and is probably identical with an immature *Synbothrium* from the spiral valve of *Trygon centrura*, which the same author describes† as a new species under the name of *Syndesmobothrium filicollis*. In view of Linton's descriptions and figures I have not thought it necessary to describe the structure of the fully-formed scolex, but proceed at once to the description of the developmental stages I have been able to examine.

Fig. 14 represents a median longitudinal section of the youngest blastocyst observed. It had an elongated form of uniform thickness, except for a slight constriction near its middle, and measured 7.5 mm. in length by 1 mm. in breadth. The blastocyst in its natural position is surrounded by an outer fibrous layer derived from the peritoneum, and representing the cyst of the *Cysticerci* properly so-called. The part enclosed by the cyst, and here, after Linton termed the blastocyst, really represents the caudal vesicle of these forms, and is, without doubt, the direct derivative of the embryo. The blastocyst is in the fresh condition of an opaque whitish colour and contains scattered calcareous corpuscles.

The structure of the blastocyst is comparatively simple. It is invested by a thin layer of cuticle; below this is a thin granular layer with scattered nuclei. Internal to this is a vacuolated tissue, with here and there scattered nuclei, calcareous corpuscles, and a series of longitudinally running fibres, by means of which the contractile movements of the living blastocyst are probably performed. The central mid-portion of the blastocyst is occupied by a somewhat irregular cavity. Two well-marked excretory vessels with thin cuticular walls run along, one on either side of the blastocyst, to its posterior end, where they unite to open to the exterior by a short terminal canal.

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\* "Notes on two Forms of Cestode Embryos," *American Naturalist*, 1887, p. 199.

† "Notes on Entozoa of Marine Fishes," United States Commission of Fish and Fisheries, 1891, p. 861, pl. xv. figs. 2-4.

The first stage in the development of the scolex is the appearance, at what will become the anterior end of the blastocyst, of a narrow involution. It is lined by a thin cuticle continuous with the outer cuticle, while the granular layer below it is likewise continuous with the similar layer below the external cuticle, only here it is somewhat thicker and contains a large number of small deeply staining nuclei. The first stage in the development of the *Synbothrium* scolex is thus identical with the corresponding stage in the development of the *Cysticerci* properly so-called.

Fig. 15 shows a further stage in the development of the involution. It is now considerably larger, and the granular layer surrounding it is thicker and contains far more numerous small nuclei. The internal tissue of the blastocyst now forms a more compact mass around the involution, while the central cells have for the most part disappeared. At the bottom of the involution cavity, which now communicates with the exterior by a narrow opening, is seen a small elevation, probably the first indication of the scolex.

Fig. 16 is a longitudinal section of an older cyst, about 5.5 mm. in length by 1 mm. in breadth at its anterior end. This anterior or scolex-containing end is broader than the posterior end of the blastocyst, and is now marked off from it by a well-marked constriction. The involution cavity is now very much larger than in the preceding stage and communicates with the exterior by a well-marked though narrow canal. The involution cavity is lined by a very thin cuticle, and arising from its bottom is a knob-shaped mass, the rudiment of the scolex. That this knob-shaped mass gives rise to the whole of the scolex is evident when we compare the mode of attachment of the fully-formed scolex (Fig. 5) with that of the scolex bud. In both cases they are attached to the centre of a saucer-shaped area of tissue, which thins out at the edges and has the concavity directed towards the aperture of invagination. The *Synbothrium* scolex does not then arise directly from the invagination sac, but by the differentiation of a

bud which arises from its floor, thus confirming Hoek's\* view that "Der Scolex entsteht dan bei *Tetrarhynchus* auf dem Boden dieser Einstülpung aus knopfförmiger Anlage," and also Wagener as quoted by Leuckart†—"If we imagine the thimble-like projection from the base of the sac broadened out above like a mushroom, we have the head of a *Dibothrium*, which might become a 'dibothrian' *Tetrarhynchus* by the addition of proboscides."

Leuckart,‡ on the other hand, considers "that it is the sac-like invagination of the bladder itself which produces the head. The elevation always appears only as a secondary structure of subordinate morphological importance, and is, moreover, by no means so widely distributed as the statements of some investigators would lead one to suppose." He bases this view on an examination of young *Tetrarhynchus* bladders from *Lophius piscatorius*, in which he finds, "that the elevation only takes place at a time when the suctorial cups and proboscides are already formed and when the head, with its different parts, is thus essentially mature." If this be so in the case he examined, then we must admit that in the *Tetrarhynchidae*, as among the *Tæniadæ*, the head may arise in two distinct ways. It may arise directly from the invagination sac or it may arise as a bud from the bottom of the invagination sac. The occurrence of the latter of these two methods is denied by Leuckart, but Moniez,§ from the examination of *Cysticercus pisiformis*, is convinced "que la tête du Cysticerque bourgeonne au fond de l'invagination comme l'avait indiqué Wagener," and Hamann|| has also described and figured (*cf.* especially his fig. 5, taf. 1.), in the development of the Cysticercoid of *Tenia sinuosa* from *Gammarus pulex*, a plug-shaped structure which arises by

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\* "Ueber den encystirten Scolex von *Tetrarhynchus*," *Niederländisches Archiv für Zoologie*, B. v. p. 3.

† *Loc. cit.* p. 374.

‡ *Loc. cit.* p. 375.

§ "Essai Monographique sur les Cysticerques," p. 36

|| "In *Gammarus pulex* lebende Cysticerkoiden mit Schwanzanhängen," *Jenaische Zeitschrift*, Bd. xxiv. p. 2-3, taf. 1. figs. 4-8.

the inturning of a cushion-like thickening of the bottom of the invagination sac into its interior. Concerning the further development of the plug he says: "An diesem Zapfen spielen sich die weiteren Veränderungen ab, an ihm bilden sich die Saugnäpfe und der Hakenkranz."

The matter is well summed up by Villot\*: "La vérité est que la tête des Cystiques peut se développer de deux manières bien différentes," and we can now extend Villot's view to the *Tetrarhynchidae*.

Returning now to the scolex-forming bud in *Synbothrium*, at the stage under consideration the bud is typically knob-shaped, being attached to the bottom of the involution sac by a narrow stalk, which widens out into an expanded and rounded head. It consists of a fairly compact mass of small rounded cells, such a tissue among the Cestodes having, according to Moniez,† all the characters of cells in process of reproduction. In the anterior broader portion of the bud there are large clear spaces, and the small cells are not so numerous; in the stalk the tissue is of a denser character, the cells being more numerous and larger. In the anterior region are seen two denser areas radiating outwards. These are in all probability the fundamentals of the proboscides. Below the cuticle of the blastocyst at this stage an external layer of circular fibres and an internal layer of longitudinal fibres can be recognised; then internal to these is the granular layer containing nuclei lying at some distance from each other; the cell boundaries are not distinct.

Fig. 17 is a longitudinal section of the next stage I have been able to obtain. It is separated by a somewhat wide interval from the preceding stage, for the knob-shaped process has not only given rise by elongation to the external form of the adult scolex, but internal differentiation has advanced to a considerable extent. The cyst, of which Fig. 17 is a longitudinal section, had a length of only 3.5 mm., so that the size of the cyst is evidently not

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\* Cystiques des Ténias, p. 20.

† Loc. cit. p. 37.

indicative of the stage of development of the scolex. In this stage the three parts into which, after Lang,\* the adult scolex can be divided can readily be distinguished. These parts are: (1) The anterior or head region, which carries the bothridia; (2) The middle or neck region, through which run the proboscis sheaths; (3) The posterior region, in which the proboscis bulbs are situated. The internal parts, however, are still in process of differentiation, and the cuticle investing the scolex is still a comparatively thin layer.

In the posterior part of the scolex the proboscis bulbs are represented by non-staining tracts apparently of a fibrous nature and surrounded by deeply staining cells. Such cells occur along the whole course of the proboscides and sharply mark them off from the surrounding cells. In the middle region of the scolex occur longitudinally running cellular strands surrounded by deeply staining cells similar to those round the bulbs. These cellular strands probably give rise to the retractor muscles of the proboscides, while the deeply staining cells form the sheaths of the proboscides. Anteriorly the proboscides themselves (Fig. 17, *prb.*) are seen to be hollow structures with well-defined cuticular walls and surrounded by deeply staining cells. On the interior of the hollow proboscis the hooks appear as small inwardly-projecting conical processes of its cuticular wall.

In sections of a cyst slightly older than the preceding, the proboscis bulbs are now found to possess very definite fibrous walls, enclosing a cellular strand, from which the retractor muscle will be developed. The wall of the bulb is very much thicker on its inner face than externally and closely surrounds the cellular strand, the large cavity found in the bulb of the fully-formed scolex being not yet formed. The proboscis, surrounded by a layer of deeply staining rounded cells, is now found to lie in a definite cavity, the cuticular wall of which forms the proboscis sheath. Posteriorly the sheath becomes continuous with one of

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\* MT. Zool. Stat. Neap. ii. 1881, pp. 372-400; see résumé, Journal of the Royal Microscopical Soc. 2nd Ser. Vol. ii. part 1, 1882, 51.

the bulbs, while anteriorly it opens to the exterior beside one of the bothridia. The hook fundaments have now become separated off from the cuticular wall of the proboscis and appear as short inwardly-projecting processes with rounded ends. These by subsequent elongation give rise to the long and slender hooks of the adult scolex. The cellular strands in the bulbs are continuous with similar strands which run through the hinder parts of the proboscis sheaths and become continuous with the proboscides themselves. As development advances, well-marked obliquely-crossing fibres are developed in the walls of the bulbs, which now enclose large cavities. From the cellular strand the retractor muscle is developed; anteriorly it is continuous with the proboscis, while posteriorly it passes back to become inserted into the posterior end of the cavity of the proboscis bulb.

The blastocyst, when the scolex has reached the fully-formed state, has an elongated club-shaped form, the largest found measuring 14 mm. in length. The anterior club-shaped end contains the scolex, attached by its posterior end to the bottom of the invagination sac. Round its point of attachment a number of minute hair-like processes of the cuticle are developed. The scolex is surrounded by a fluid containing granules and probably nutritive in function. As the scolex lies naturally in the invagination cavity, its parts have the following disposition: the posterior part lies in a line with the long axis of the blastocyst; the neck curves round, forming a loop lying on the straight posterior portion, while the head lies on one side.

I append some notes from Linton's\* description of the scolex as explanatory of fig. 19, which is a drawing of the adult scolex freed by mechanical means from the blastocyst:—The head is tetragonal, transverse, cruciform. Bothria four, subcircular, convex, cup-shaped, each the termination of a short cylindrical pedicel. They are arranged in a cruciform manner, but also somewhat in pairs, and capable of being directed either forwards or backwards in pairs. Proboscides very long and slender, each one running

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\* *Loc. cit.*, "Notes on Entozoa of Marine Fishes," p. 861.

through a pedicel and emerging at the apex, apparently beside the bothrium proper; neck very long and slender, cylindrical, enlarging slightly at the contractile bulbs and rounded at the base, tapering to a point where it is connected with the body (blastocyst); proboscis sheaths spiral, contractile bulbs linear, oblong: hooklets long and slender, falcate. Size of scolex 4.60 mm. Hooks near the middle .06 mm. long.

#### RÉSUMÉ.

(1) The so-called blastocyst or endocyst is the serial homologue of the caudal vesicle of the Cysticerci.

(2) The wall of the invagination sac represents the body of these forms.

(3) The scolex, consisting of head and neck, arises from the bottom of the invagination sac as a knob-shaped process, which, by subsequent elongation and internal differentiation, gives rise to the fully-formed scolex.

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### EXPLANATION OF PLATES.

#### PLATE III.

Figs. 1-6.—*Piestocystis Hoplocephali*.

Fig. 1.—Transverse section of the wall of Hoplocephalus cyst. Zeiss. D., oc. 1, cam. luc. *h. l.*, homogeneous inner layer of wall ("blastogen"); *l. l.*, middle laminated zone; *f. l.*, outer fibrous layer.

Fig. 2.—Longitudinal section (nearly median) of Cysticercus from Hoplocephalus, with partially evaginated head. From a specimen preserved in corr. subl. and stained with cochineal. Zeiss. A., oc. 1, cam. luc. *f. s.*, frontal sucker; *b. c.*, bladder cavity; *l. f.*, longitudinal elastic fibres; *t. c.*, terminal canal of excretory system.

Fig. 3.—Transverse section of a Cysticercus with invaginated head, at the level of the suckers. Corrosive sublimate and Ehrlich's Hæmatoxylin. Zeiss. A., oc. 1, cam. luc.; details with Zeiss. D. c., cuticle; *s. c.*, subcuticula; *r. c.*, "receptaculum capitis"; *e. f.*, elastic fibres; *a. v.*, ascending vessel of excretory system; *d. v.*, descending vessel; *i. v.*, invagination cavity of head.

Fig. 4.—Portion of a transverse section (slightly oblique) of a *Cysticercus* with invaginated head, passing through frontal sucker. Chromosmic acid and Ehrlich's Hæmatoxylin. Zeiss. C. and oc. 1, cam. luc. *f. s.*, frontal sucker; *c. s.*, cavity of sucker; *c. f.*, circular fibres; *r. f.*, radial fibres; *l. s.*, lateral sucker.

Fig. 5.—Outer portion of a transverse section of a *Cysticercus* about its middle region. Corrosive sublimate and Ehrlich's Hæmatoxylin. Zeiss. D., oc. 1, cam. luc.; details with Zeiss. F. *c.*, cuticle; *c. f.* and *l. f.*, circular and longitudinal fibres of dermo-elastic layer; *s. c.*, subcuticula; *r. c. c.*, cavity with remains of calcareous corpuscle; *g. t. c.*, cells of ground tissue; *m.*, matrix; *e. f.*, elastic fibres.

Fig. 6.—Outer portion of a longitudinal section. Corrosive sublimate and cochineal. Zeiss. F., oc. 1, cam. luc. *c. c.*, outer and inner layers of cuticle; *c. n. c.*, cavities containing a number of small calcareous corpuscles.

#### PLATE IV.

##### Figs. 7-11.—*Piestocystis Lialis*.

Fig. 7.—Cyst from *Lialis* containing three *Cysticerci* ( $\times 50$ ).

Fig. 8.—Longitudinal section of cyst ( $\times 100$ ). *f. l.*, fibrous outer layer of wall; *h. l.*, homogeneous inner wall; *c. n.*, connective tissue network; *ct.*, *Cysticercus* cut obliquely; *c. ct.*, cells attached to inner lining of cyst and probably representing the first stage in the development of a *Cysticercus*; *c. cp.*, columnar epithelium of intestine.

Fig. 9.—Invaginate *Cysticercus*, from a specimen preserved in Flemming's Fluid ( $\times 80$ ).

Fig. 10.—*Piestocystis Lialis* with evaginated head; partly from living specimen ( $\times 50$ ).

Fig. 11.—Transverse section of invaginate *Cysticercus* at level of suckers ( $\times 260$ ). *c.*, cuticle; *s. c.*, subcuticula; *l. f.* longitudinal fibres of dermo-elastic layer; *g. t.*, ground tissue; *i. v.*, invagination cavity of head.

#### PLATE V.

##### Figs. 12-13.—*Monocercus Didymogastris*.

Fig. 12.—*Monocercus Didymogastris* in optical longitudinal section ( $\times 250$ ). *bl.*, "blastogen"; *c. v.*, caudal vesicle; *b.*, body; *r.*, rostellum; *s. r.*, sheath of rostellum; *s.*, sucker.

Fig. 13.—Isolated hook of *M. Didymogastri* Zeiss. F., oc. 3, cam. luc. ( $\times 900$ ). *a. r.*, anterior root; *i. r.*, internal root; *f. p.*, free part of hook.

Figs. 14-19. —Development of Scolex of *Synbothrium*.

Figs. 14-18 are longitudinal sections of the anterior ends of blastocysts of different ages. Drawn with Zeiss. A., oc. 1, cam. luc.; details with Zeiss. D., oc. 4.

Fig. 14.—Longitudinal section of youngest blastocyst observed, with developing invagination cavity.

Fig. 15.—Further stage in development of same.

Fig. 16.—Longitudinal section of blastocyst, with the knob-shaped process arising from bottom of invagination cavity.

Fig. 17.—Longitudinal section of blastocyst, with developing scolex. *prb.*, proboscis with developing hooks.

Fig. 18.—Longitudinal section of blastocyst, with fully-formed scolex in invagination cavity. *br.*, bothridium; *pr.*, proboscis lying in cavity of proboscis sheath; *pr. b.*, proboscis bulb; *r. msc.*, retractor muscle; *i. v.*, invagination cavity; *w. i. v.*, wall of invagination cavity.

Fig. 19.—Fully-formed scolex of *Synbothrium*, separated mechanically from the blastocyst ( $\times$  about 30).